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The American Midland Naturalist

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THE ANATOMY OF STENOBOTHRIUM MACROBOTHRIUM, DIESING.

FRANCIS J. WENNINGER, C.S.C.

The work reported in the following pages contains the results of an investigation carried on in the laboratory of the First Institute of Zoology of the University of Vienna, and was accepted by the faculty of that University in part fulfillment of the requirements for the degree of Doctor of Philosophy. The work was suggested in outline by Dr. Theodore Pintner, professor and head of the Institute, who placed at my disposition valuable personal material as well as the resources of the Institute and was ready at all times to interrupt his own investigations to assist me in every way. I wish here to acknowledge my indebtedness to Professor Pintner and to thank him sincerely for his help.

I am grateful also to Dr. Frederick von Querner, the able assistant of Professor Pintner, for his help in making the plates that illustrate the text.

Arabic numbers occurring in the text refer to the corresponding numbers in the bibliography.

Stenobothrium macrobothrium has been known to science since the time of Diesing, in 1863, though, up to the present,

no study of its anatomy has been made. The species appears under the following names:

Tetrarhynchus bicolor, Bartels
Bothriocephalus bicolor, Bartels
Tetrarhynchobothrium bicolor, Diesing
Stenobothrium macrobothrium, Diesing

The literature hitherto published concerning the occurrence of the species includes lists of museum material, with indications of the origin, as well as records of actual finds together with dates and names of hosts. The following is a resume of the information available on the subject.

I. Material from the Imperial and Royal Museum of Natural History in Vienna. This material is preserved in five glass containers. A short description of the material, including labeling and numbering follows.

1. "Stenobothrium appendiculatum, Rud. Salmo salar. hip. 651." This is a single poorly preserved specimen of a larva having a total length of 5 mm. Four millimeters of the entire length is scolex and collar, leaving only a single millimeter for the appendage. The width of the specimen is one millimeter. No further data are given. The place of origin is not indicated.

2. "Tetrarhynchobothrium bicolor, Diesing. Orig. Coryphaena hippuris tun. ventr. 652." Numerous well preserved yellowish-white larvae together with pieces of the wall of the stomach. There are also some encysted in the stomach tissue.

3. "Tetrarhynchus. Ceylon. 667." This consists of pieces of digestive tract (stomach ?), probably of a selachian. The pieces are highly muscular, and the inner surface is longitudinally folded or furrowed. Here there are masses of proglottids, relatively well preserved, with their large rust brown, violet to black scoleces. Intermingled with the specimens and also attached to the intestinal wall are large chains of the species Anthocephalus elongatus. (Pintner, 2; 777 and 3; 191-192.)

4. "Tetrarhynchobothrium bicolor, Bartels. Larvae Pelamys sarda inter muscl. Dschidda, 12105." Many well preserved larvae.

5. "Cestodes. (6 S. Br. 8 O. Lng.) West Africa. Tetrarhynchus

bicolor, Bartels. Pelamys sarda musc. 12106." Contains a trunk and fragments of fishes with encysted and free, well preserved larvae.

II. Material from the Royal Museum in Berlin. This material is contained in ten glass bottles. The following is a list of the contents with data appended to each container.

6. "Tetrarhynchus from Carcharias 12 S. Br. 42 O. L. gr. East Africa Collector, Dr. Fischer. 1104." Several large chains and portions of chains with scoleces.

7. "Tetrarhynchus macrobothrius, Rud. T. papillosus. (Types.) Coryphaena hippuris, Tun. ventriculi. Brazil. Collector, Natterer. Collection Rudolphi, 1704." Five pieces of brown larvae.

8. "Tetrarhynchus macrobothrium, Rud. (Type) Testudio midas. Tun. ventric. Berlin. Coll. Rud. 1705." One brown larva which has the appearance of having once been allowed to dry up.

9. "Tetrarhynchus macrobothrius, Rud. Coryphaena hippuris, Tun. ventric. Coll. Rudolphi. Collector, Natterer, 1706." Two larvae apparently fastened to the wall of the stomach by the proboscis.

10. "Tetrarhynchus macrobothrius, Rud. Coryphaena hippuris ? Brazil. Coll. Rud. Collector, V. Olfers. 1707." Five typical larvae of 4-7 mm. in length. The longest is 2 mm. broad, resembling a cylinder rounded off at both ends.

11. "Tetrarhynchus macrobothrius, Rud. 1712." Several larvae turned brown. One of these shows behind the anterior end two deep furrows, resembling pronounced contraction waves. Two specimens are fastened together at the broad sides, and face in opposite directions. One specimen has penetrated with its proboscis, and with a portion of its anterior end, into another specimen. Some such phenomenon may account for the pincher-like appearance of another specimen. It might be stated here that this mutual attachment of specimens by means of a sucking apparatus is not to be interpretated to mean that the specimens have necessarily occupied the same hollow space in the host. Specimens that have been artificially released from the intestinal wall or from their cyst, and have been placed into a watch glass, begin to move as though they were seeking some object for attachment. If such an object is not found, there will be mutual attachment, and this will take place so vehemently that the animals cannot be separated without injury to one or both animals concerned. This has been observed in *Tetrarhynchus lingualis* in sea water, in *Calliobothrium coronatum* in the intestinal tract, and in *Gorgodera cygnoides* in physiological salt solution. In this last vial there is also a peculiar monstrosity. A scolex of about 4 mm. in length, instead of being followed by a single strobila, has two strobilae,

each of which has its own bladder. This recalls a case of scolex polymorphus observed some years ago by Pintner, in which there were two bladders lying side by side. The peculiarity of the case consists in this that the two strobilae, one of which already shows striations, overlie each other in the dorso-ventral position. The contact is not entirely continuous, but the contraction of the individual is sufficient explanation for this. Definite information concerning the position of those animals as well as of the development of the tail where rings are invisible could be obtained only by sectioning. This involves the destruction of the material. The report of Pintner seems to be the only one on record.

12. The label reads "T. bicolor" and this is correct. But the catalogue has "T. lingualis, Cuv. Wagner diagn. 1714." This is incorrect and can probably be explained on the assumption that the material was transferred from one container to another. The material consists of proglottides which are poorly preserved.

13. "Tetra. origin (?) 1720." This contains several macrobothrius larvae, and one small attenuatus. Some of the macrobothrii are encysted. Some of the larvae, within the cyst, are surrounded by a very fine secondary membrane.

14. "F. 488. Tetrarhynchus macrobothrius, Rud. Scolex, Ballistes, etc." This is a collection of entirely macerated and worthless fragments that have no relation whatever to our specimen.

15. "F. 489. T. macrobothrius, Rud." One larva.

16. "In Squalus, large intestine. Auckland." Many large and beautiful chains with scoleces. Among the material were chains 27 to 38 mm. in length, 8 to 9 mm. of this total length is scolex. The bothridial portion measures 6 to 6.5 mm., the postbothridial 2.5 mm., and the width is 2 to 3 mm. The specimens very probably were collected by the Novara Expedition.

The following is a resume of data available on hosts and places of origin:

(a) LARVAE. The cases 7 and 9 might be identical, though two different places of origin might be supposed. It is not unlikely that case 2 is identical with cases 7 and 9. Case 10 is an independent find. We have, therefore, the larvae of at least two and perhaps even of three or four finds from the peritoneal cysts of *Coryphaena hippuris*, all of them probably from the coast of Brazil. Two finds come from the musculature of *Pelamys sarda*, one from the Red Sea and one from the Atlantic, somewhat east of Ascension. The cases that are peculiar are

case 1. from the liver of *Salmo salar*, with no place of origin given, and case 8. *Testudo midas*, found in Berlin, by Rudolphi.

(b) CHAINS. Case 6 gives an indication as to the manner of procedure for determination, for here *Carcharias* is mentioned as the host. Likewise case 16 is significant,—"Squalus, large intestine." It is, therefore, the larger sharks that are to be considered as the final hosts. In case 6, the specimen was found between the north peak of Madagascar and Africa. The second place of origin mentioned, though without a mention of the host, is the Indian Ocean. Case 16 mentions the vicinity of New Zealand. The conclusion seems to be warranted, therefore, that the final host of our species is to be found among the larger sharks and among the wanderers rather than among the coast forms. The intermediate hosts are *Coryphaena hippuris* and *Pelamys sarda*. In the latter, the parasite was found in the peritoneal cysts or in the musculature. Infested specimens seem to abound in the tropical and subtropical seas.

For the sake of completeness, the places of occurrence in the United States are here appended. This information was compiled from records of various authors as published in the reports of the National Museum and the Fish Commission.

The larvae of the species have been reported as follows:

From *Coryphaena hippuris*, the Dolphin, (No. 5483, U. S. N. M.). Collected from the Gulf Stream on August 13, 1885. Numerous on peritoneum and mesentery. The alcoholic specimens vary in length from 4 to 8 mm., and in shape from ovate to oblong linear, according to the state of contraction. The larger specimens have distinct bothridia.

From *Xiphias gladius*, the Swordfish. (No. 4820, U. S. N. M.) Collected off Martha's Vineyard, Mass., on July 25, 1887. Lodged in the peritoneum. Three larvae of this lot were found with their proboscides penetrating the tissues of *Rhynchobothrium attenuatus*, with which they were associated. Length of the living specimen 10.5 mm. Dimensions of one alcoholic specimen length, 6 mm.; diameter, 1.25 mm.; length of proboscis, 0.56 mm.; length of proboscis sheath, 1 mm.; diameter of proboscis at base, exclusive of hooks, 0.08 mm., at apex, 0.07 mm.

From the same host, on July 15, 1904, many on viscera, in

each of four swordfish, mostly yellowish-white, some ivory white; active; 6 to 12 mm. Also on July 13, 1911, ten globular cysts on viscera. Finally on July 20, 1912, one from viscera.

From *Carcharius obscurus*, the Dusky Shark. (No. 4817, U. S. N. M.) Collected at Woods Holl, Mass., on August 12, 1887. The specimen was found adhering to the mucous membrane of the pylorus. The stomach wall was locally inflamed where this parasite was attached. There was also another ulcerated spot in mucous membrane nearby. The specimen was quite active when removed. Dimensions: length, 7 mm.; diameter of the anterior portion, 2 mm.; diameter of the middle portion, 2.5 mm.; diameter of the posterior portion, 1.5 mm.; diameter of the posterior appendage at the beginning of the strobila, 5 mm.

From *Galeocerdo tigrinus*, the Tiger Shark. (No. 4825, U. S. N. M.) Collected at Woods Holl, Mass., on August 14, 1889. Specimens from the stomach. Dimensions: length, 5 mm.; maximum diameter, 1.4 mm.; length of the proboscis, 1 mm.; diameter at base, 10 mm.; diameter near middle including hooks, 08 mm.; length of hooks, 026 mm.

Four specimens from the peritoneum and mesentery of *Xiphias gladius*, the Swordfish. (No. 4829, U. S. N. M.) Label reads, "September 21. Trawlline, U. S. Fish Commission."

From *Echeneis naucrates*, the Sucker. On August 31, 1920. Five white globular cysts, 3 mm. in diameter, from the serous coat of the stomach and intestines.

From *Lophius piscatorius*, the Goosefish, on July 29, 1910. One specimen, 7 mm. long.

From *Sarda sarda*, the Bonito. Two specimens under the peritoneum. June 27, 1910.

The following data have been compiled on the adult parasites of our species. Where no other locality is indicated, Woods Holl, Mass., is to be understood.

From *Charcharinus obscurus*, the Dusky Shark.

1905, August 14. Two; head and neck, including collar of one, deep

purplish red; strobilas 30 and 45 mm. respectively. A fragment of the strobila measured 110 mm. in length; largest proglottides, length 1.2 mm., width 3 mm., length of ehad and neck 6.5 and 9 mm.

1907, July 31. Two in shark, measuring 183 cm; one of the worms was firmly attached to the mucous membrane. Length of the longer in sea water was 200 mm.; length of the scolex at rest 11 mm; stretching to 20 mm.; diameter, 1.75 mm. The face of the strobila on which ova lie is convex, the opposite side is concave. Ova variable, but the larger ones measuring .031 by .024 mm. Shells of the ova are very thin.

From *Galeocerdo arcticus*, the Arctic Shark.

1905, August 26. Three scoleces adhering to the mucous membrane of the stomach.

1913, August 13. One attached to the mucous membrane of the stomach. Length of the scolex, 5 mm.; of the strobila, 6 mm.; segments beginning short and much narrower than the scolex.

1914, August 12. Six scoleces from the mucous membrane of the stomach. At one point where some of the parasites were attached there was considerable suppuration. All were short, but one showed the beginnings of a strobila. This one measured 18 mm. in length; no segments.

1915, August 6. Associated with *T. bisulcatus;* a number of them being attached together near the anterior end of the stomach in a pit of the mucous membrane which was abraded and inflamed. (U. S. N. M., Helm. Coll. 1721.)

From *Coryphaena hippuris*, the Dolphin.

1899, August 23. One encysted in the peritoneum.

1902, August 1. Two from cyst in stomach wall.

From *Galeocerdo tigrinus*, the Tiger Shark.

1899, August 19. Several attached to and penetrating the stomach wall.

From *Carcharinus Milberti*, the Blue Shark.

1922, July 10. One specimen attached to the wall of the spiral valve.

From *Paralichthys dentatus*, the Flounder.

1899, August 15. One in material washed from the alimentary canal.

The data presented seems to warrant the conclusion that *Stenobothrium macrobothrium* is a cosmopolite, and that its hosts are exclusively members of the shark family. There

seems to be only one record of the occurrence of the parasite in a host that does not belong to this family. This suggests that perhaps due to an interchange of materials or to some other cause, there is here at least the possibility of an error.

Adults and larvae of old museum material can be recognized and differentiated by their coloration. Adults invariably have the anterior portion, that is, the head and a considerable portion of the scolex, colored a deep black. The color may be equally and uniformly distributed, or it may appear in spots and stripes. The coloration of the head frequently ceases abruptly at the juncture of the head and neck and is confined to that portion of the head which is anterior to the neck proper. Occasionally there are isolated patches of color, or even entire stripes on the strobila. The quality and intensity of the coloration seem to depend both on the medium in which the specimens are preserved as also on the light. The color varies from a violet to a dark brown to black. The first impression one gets is that the entire phenomenon is one of incrustation. Indeed, the microscope shows very fine needles and spicule-shaped crystals which appear opaque and entirely black and do not resolve in the light. These crystals seldom appear singly but nearly always as star-shaped, cross-shaped or even globular. In all these various arrangements, the needles always converge at a given point. They lie at a depth of only a few micra from the cuticle, though a few crystals may penetrate the cuticle or may even lie on the body surface. It may be stated, however, that this latter condition is found only in old material in which the integument is either badly injured, or from which it has almost entirely disappeared. It may also happen that individual bundles of crystals are pulled to the periphery by the knife of the microtome. Single strands or wire-like structures appear in the interior of the body, especially near or actually in the tissues of the great lateral trunks of the nervous system. Here they suggest an unsuccessful Golgi stain.

The black structures do not seem to belong to any particular tissue, or to particular cells, nor to the skeletal sub-

stance, but seem to be a substance that partakes of the nature of a colloid sediment formed by combination of a foreign fluid with the fluids of the body.

Larvae that are still enclosed in cysts, or such as have only recently been removed from cysts, are colorless. But even in these forms, pigmented needles are sometimes found. These are isolated and not arranged into bundles, are still transparent, and lie on the outer stratum of the body, apparently on the surface.

All these appearances give the impression of a precipitate artificially formed. However, they occur in all specimens, and in all collections without exception. This constant recurring of the phenomenon induced Bartels, Diesing and Dujardin to recognize the specific name *bicolor*. The occurrence of pigmentation in larval forms seems to indicate that neither the nature of the intestinal tract nor the character of its contents is of any consequence in the formation of the pigment.

A microchemical analysis made by Molisch of Vienna was published by Pintner in 1914. But the examination of the Valdivia material shows that the composition of the pigment is not the same as that previously reported from other museum material. There is a notable lack of intensity,—to mention only one of the macroscopic differences. The impression one gets at first sight is that created by the pigmentation ordinarily met with in all Cestode material. In sections, this pigment appears not as crystals but as minute, black, opaque globules that are seldom isolated but appear as irregular masses. The distribution of the pigment itself is essentially irregular and is to be found principally between the longitudinal muscles and the outer zone of the excretory system. The denser distribution is always towards the periphery. This seems to indicate that the velvet sheen of the coloration of old specimens comes from small crystalloid structures. There seems to be no other explanation possible than this, that during almost a century during which the specimens have lain in preservative fluid, the granular pigment became crystalized. In view of the fact that most of the specimens of the Valdivia

Expedition were either in formaldehyde or corrosive sublimate or in alcohol, as was the case with the oldest specimens, as well as because of the fact that all the specimens were rinsed in water before fixing, this explanation seems the most plausible.

Before entering upon the subject matter itself of this treatise, an explanation of the terminology followed will be useful. The terms used here were first enployed by Pintner. (36) There can hardly be any question of their entire appropriateness and general usefulness. They are appended here in the hope that a more general knowledge will lead to a more general appreciation and eventually adoption.

Pars bothridialis scolecis (pbo) designates that anterior portion of the head which carries the four bothridia.

Pars vaginalis (pv) is that portion of the head-stalk or peduncle (Kopfstiel) which bears the proboscis sheath.

Pars bulbosa scolecis (p. bulb.) is that portion of the head in which the muscle clubs of the proboscis are situated.

Pars post bulbosa scolecis (p.pb.) is the term used to designate all the remaining portion of the head.

A chain of segments is called *apolytic* or *anapolytic* according as the individual proglottids either break off automatically or not. An *apolytic* chain may be *eupolytic* or *hyperpolytic* according as the various segments continue to develop or not after breaking off from the chain.

The terms *craspedote* and *acraspedote* are used to designate the manner in which the various segments of a chain fit into each other. The presence of a velum in the preceding segment which fits into a succeeding one is indicated by the term *craspedote;* the absence of this velum is expressed by the term *acraspedote.* In the former case there will be left a toothed margin; in the latter case, the margin will be straight-lined.

The genus *Stenobothrium* of which *macrobothrium* is a species has the following characteristics. There are four bothridia. Of these, two belong to a dorsal and two to a ven-

tral group. Their margins are fitted up with minute hairs. The scolex is craspedote. The proboscides are poorly developed. The individual proboscis is thin, short, thread-like, with similar small hooks which are relatively widely spaced. The sheaths are short and thin, and the clubs are small. These latter are composed of numerous small and very thin muscles contained in six cups, each of which is, in turn, composed of several layers of muscles. The musculature of the clubs on cross section is, to use Pintner's phrase, arranged after the manner of four horses running apace in the ring, with the thinnest portion of the head representing the rear of the horse.

The strobila is anapolytic, with all the segments, even the last, wider than long. Margins are entirely smooth-rimmed, and flanked on both sides by straight lines.

The genital cloaca is located at the anterior margin of the segment, but in a ventral position, with its end turned backward. The uterine openings are median and run in a straight line. The uterus is many-branched and ventral in position, while the testes are dorsal. The ovaries consist of structures resembling in arrangement the wings of a butterfly. There are five or six discernible layers. The connecting tubules are frequently so thin that only a single egg can pass through at a time. (Fig. 9.)

At the end of each segment there is a muscular septum. (Fig. 4.) The primary end segment bears a conical plug which is protrusible from the bladder and may be villous, as in *macrobothrium*, or papillated, as in *linguale*. A final character, and one first reported by Pintner in 1928, is the presence of a bladder in each segment. (38)

Macrobothrium illustrates all the characters just mentioned as generic. The special and specific characteristics will be indicated as they are met. The species occurs in considerable numbers in the sharks. The material examined for purposes of this report all came from one species of host,—*Carcharias lamia*, but the literature on the subject mentions specifically fourteen other hosts for this Cestode. There is

considerable variation in the size of individual specimens, the total length ranging from 32 to 230 mm. The last measurement is given by Linton. (21) The longest of my specimens measured only 82 mm. and had 140 segments.

The head of *macrobothrium* has been described in outline by Pintner. (33) For purposes of completeness, a short resume of his report is here appended. The head is subconical and bluntly rounded in front. It averages 12 mm. in length, is thin and craspedote. There are four bothridia, two being dorsal and two ventral. The pars bothridialis measures about 12 mm. This represents the most excessive elongation known among the Tetrarhynchoids. Indeed, in this species, the head attains a length which is several times greater than that of all the remaining portions. The pars vaginalis is contained in the pars bothridialis. The pars bulbosa measures .06 mm., and the pars post bulbosa measures 4 mm. The proboscides are poorly developed. They are thin, short, thread-like, about a millimeter long, with uniform, widely separated hooks arranged in spirals, each spiral bearing about seven solid hooks. The bothridia are rudimentary.

The chain of segments is anapolytic, usually much attenuated anteriorly and unjointed for a short distance back of the head. Fine transverse lines soon appear, and, shortly after, the first segments are formed. The latter are usually much broader than long and are invariably rectangular in outline. There is a marked dorso-ventral differentiation. Individual segments are from 2.5 to 3 mm. broad, while one of the last segments measured .025 mm. in length.

The cirrus always opens laterally and marginally, irregularly alternate. (Fig. 2, 6.) One specimen that measured 44 mm. in length showed 54 openings of the cirrus between the 65th and the 119th segments. Of these, 30 openings were on one side and 24 on the other. More than four consecutive openings were never found on one side. The cirri are entirely withdrawn into the sheath, or they protrude more or less. The cirrus sac runs along the anterior margin of the segment, with its apex bent backwards. The cirrus and its sac are in-

variably half as long as the width of the including segment.

The vagina is dorsal to the cirrus and a little to the rear where it frequently breaks through the mass of the vas deferens. (Fig. 6.) The genital cloaca lies towards the anterior margin and somewhat ventral. The uterus is branched and lies on the ventral side. The uterine openings, which are never preformed, lie in a median line, strictly one after the other. At the end of each segment there is a double-layered muscular septum. The primary end segment bears a villous or papillated plug which is extrusible from the interior of the bladder. As a special external characteristic of the species, a rather conspicuous muscular band must be mentioned. (Fig. 5.) This runs medially throughout the entire length of the individual specimens on both dorsal and ventral surfaces.

The species is clearly protandrous, i. e., the male elements reach maturity before the female elements. The primary end segments were missing in nearly all the specimens examined. A typical specimen having this end segment was found to have a total of 120 segments, and the uteri of the last 60 segments contained eggs. But portions of strobila were found in which individual segments contained no eggs at all. The explanation for this phenomenon was given so long ago as seventy years by E. Van Beneden and is quite generally understood. Many of the segments on stimulation by chemical or mechanical means, or even on mere contact with water, burst and send out streams of eggs.

The body of *macrobothrium* is composed of the tissues and organs that are generally found in all Cestoda. This paper will confine the discussion to those elements only of the integument, the muscular and excretory systems, and the organs of reproduction which seem to be peculiar to the species.

The cuticle is rather thick. Inspection with the oil immersion lens shows the presence of minute hairs covering the entire surface. Under this villous covering, the cuticle is distinguishable as a two-layered sheath. The outer layer is homogeneous in nature while the inner layer is very finely granulated. It must be emphasized, however, that the two

layers form an organic unit with no line of demarcation between them. The transition from the cuticle to the subcuticular layer is here quite apparent. The inner line of the cuticle goes over into very regular and closely fitting arcade-like structures, the fibers of which penetrate into the bodies of the subcuticular cells. To show this structure to greatest advantage, Pintner suggests a method of double staining with iron haematoxylin and orange g. The arcade prolongations are more numerous than the subcuticular cells with the result that many of them end in each cell.

The muscular system of *macrobothrium* is characteristic. Mention has already been made of the thick band of muscle that runs medially throughout the entire length of the individual on both dorsal and ventral surfaces. This is a specific character. The longitudinal muscles on either side of the median muscle number about twenty. They are about half as wide as the median band. The transverse muscles lie on the surface, above the longitudinal muscles, and seem to have about the same width throughout. On cross section, the median band is seen as a mass of muscle fibers not unlike the cut end of a cable. The mass is compact so that individual organs as, for instance, the bladder, to be mentioned more in detail later on, are diverted from their regular path or position and bent sideways. It is the median muscle, moreover, that forms the longitudinal furrow visible along the whole length of the strobila. This furrow is, perhaps, the most conspicuous single characteristic of the species when viewed macroscopically only. The peripheral longitudinal muscles are really in two layers. One, a stout layer, occurs at regular intervals and seems to give contour to the specimen. The other, a considerably weaker layer, is wedged in between the stouter layers and occurs somewhat irregularly. It is only about half the size of the stout layer. On cross section, the general appearance of these peripheral muscles might be said to be palisaded.

The excretory system in *macrobothrium* is built along the lines laid down for Cestoda in Bronn's *Klassen und Ordnun-*

gen des Tierreichs, Vol. Vermes, p. 1361 et seq. There are four main trunks and these are large enough to be seen with ordinary powers of the microscope. Since the scope of this treatise is merely that of recording deviations from type, it will suffice here to indicate in what respects deviations occur in the species examined and briefly to explain the nature of these.

The elements of structure in which *macrobothrium* differs from the type are mainly two;—first, a branching from the main trunk, which gives rise to numerous islands, and, secondly, the presence of a bladder in each segment. Both of these anatomical features are illustrated in Fig. 5. This branching is not to be understood as a mere splitting of the main trunk into smaller tubes and a further division of these into still smaller tubes till relatively minute capillaries are reached. It is rather an anastomosing of the smaller branches to meet again in a continuation of the same, the space between forming the island mentioned above.

The presence of the bladder was first noticed by Pintner. (5; 318-322.) Its occurrence in this and allied species was first announced by him in a preliminary statement published in the *Zool. Anzeiger,* Vol. LXXVI, Nos. 11-12, I. 5. 1929. He also demonstrates that this bladder must be recognized as constituting a generic characteristic.

There are on the dorsal surface of each segment several discharging vessels of the excretory system that lead through a very narrow dorso-ventrally situated passage into a bladder. In this species the bladder is evidently connected with the complicated network of canals of the system. When it reaches the large median muscle, instead of going around it, the muscle itself is bent to one side to allow for the passage of the bladder. This excretory pore may be seen also in whole mounts. Here it appears as a diagonal split. Up to the present, this aperture has not been understood. None of the various explanations have been little more than conjectures. Such is, for instance the statement that the aperture, seemingly situated at the line of union of two segments, is a

transverse anastomosis of the organs of excretion forming a vessel running in a dorso-ventral position and ending in a sort of secondary foramen. In serial sections this structure can be followed as a dorso-ventral tube. There might be some slight difficulty in locating its position with certitude as well as in differentiating it from the openings of the uterus. However, the uterine openings of *macrobothrium* are rather high up in about the middle of the segment, while the excretory pore is very definitely situated in the posterior margin. The two points that need to be emphasized in this connection are, first, the occurrence of this excretory pore in linear position on an apolytic chain of segments, and, secondly, its occurrence in the dorsal position.

The reproductive organs of all animals, their location and structure are of prime importance. This is so because the nature and structure of these organs determine to a large extent the systematic .position of the animal in question. Nearly all Cestoda are monoecious. It is also characteristic of the group that each recurring segment bears the same units of the reproductive apparatus in about the same relative position. As a rule, the Cestoda are protandrous, i. e., the male elements reach maturity before the female elements develop. One will, therefore, look in vain for testes in the posterior regions or segments, or for uteri in the anterior ones. A certain general development of the individual segments must be reached before there is any development of reproductive organs. The precise number of the segments of the strobila of *macrobothrium* in which ripe reproductive organs may be expected seems to depend, in part at least, on the total length of the specimen. I found that almost invariably the anterior third or fourth of the specimen would have no ripe proglottids, while the appearance of testes hardly ever occurred anterior to the fiftieth recognizable segment.

There are two genital openings, one for the male and one for the female organs. In *macrobothrium* these openings lie rather close together in a genital cloaca which is somewhat raised from the marginal body surface and might be called a

genital papilla. A third opening is found in *macrobothrium*, —that of the uterus.

There is no preformed uterine opening in this species, but the uterus bursts in the same place in all segments and pours out its contents. This is a factor of prime systematic importance. The laceration for the aperture always occurs in the ventral median surface of the segment. (Fig. 10.)

The male reproductive organs consist of testes, vasa efferentia, vas deferens, cirrus sac and cirrus. The literature on the genus *Stenobothrium* also mentions glands which are referred to as prostate glands. Of these I could see nothing.

The testes are innumerable. Their general position might be characterized as dorsal, though it will be, perhaps, more correct to say that they occupy the field bounded by the excretory canals in so far as this field is not occupied by other organs such as uterus and ovaries. The testes lead into the vasa efferentia, and these into the vas deferens, which is a single tube. As it approaches the cirrus sac, it becomes more convoluted, and just before it leads into the sac, these convolutions become so great as to constitute a veritable knot. The histological structure of the vas deferens seems to be very simple,—just a membrane composed of homogeneous tissue.

The cirrus sac is a muscular bag whose form, generally elongated or bottle-shaped, is subject to considerable variation due to contraction, expansion, and the influence of the strobila. Its structure is as simple as that of the cirrus,—two layers of muscle, one larger running longitudinally, the other at right angles to it and annular. Between the cirrus sac and the cirrus itself there is a parenchymatous tissue which completely fills the intervening space. It has been suggested that this loose tissue makes possible the movements of the cirrus in its sac. This seems plausible since the tissue is also permeated by muscle fibers. Moreover, the entire musculature of the cirrus sac is in direct connection with the surrounding tissue. Cross sections clearly show the connection of muscle fibers of the cirrus sac with both dorsal and ventral muscle fibers.

There are also retractor muscles present, seemingly attached at the posterior portion of the sac.

The cirrus is really a continuation of the vas deferens. It is highly muscular, being composed, like the cirrus sac, of a double muscular envelope of longitudinal and annular muscles. The wall of the cirrus seems to contain also a structureless membrane. Of the barbs, thorns and bristles mentioned by some authors, I could find no trace. When retracted, the cirrus is always convoluted. But these convolutions disappear when the organ is extruded. There seem to be no special retractor muscles. Retraction, then, would seem to be accounted for by the deturgescence of the loose parenchyma.

The female reproductive organs of *macrobothrium* consist of ovaries, oviducts, yolk glands and their ducts, shell glands and their ducts, and the vagina with the uterus.

The ovaries are glands that consist primarily of two sections connected by a middle piece. Each section resembles the expanded wings of a butterfly. Perhaps a better characterization would be to say that there is a dorsal and a ventral portion, so that a cross section of the entire organ would be represented by the letter H. (Fig. 9.) The position in the proglottis might be designated as the rear of the central field. The wings are connected only by the cross piece. The tubules are covered by a clear and apparently quite structureless membrane. The germ cells are small, with finely granulated protoplasm and large nucleus. Stained sections show the germ cells polyhedral but this is due to the pressure which they exert upon each other. In the oviducts, their outline appears oval or circular. The nucleus usually stains much deeper than the surrounding protoplasm. A nucleolus is occasionally demonstrable. This was first shown for *Calliobothrium corollatum* by Pintner as quoted by Braun. (2; 1421.) This nucleolus takes the stain about as the nucleus and appears as a crescent-shaped body in the larger germ cells. I failed to find it in any germ cells that seemed to be not yet fully developed.

The tubules of the lateral wings of the ovaries lead towards the central connecting piece. They become wider as they progress and unite in a hollow space in the connecting piece, whence the oviduct leads forward. Here a muscular apparatus is to be found, the purpose of which is to take up the liberated germ cells and to transport them onwards. Moniez, in 1881, (Bronn, 815) first called attention to this structure under the name of "Pavillon." The name "Schluckapparat" was introduced by Pintner, (Bronn, 1081) and has found general acceptance by German zoologists. There seems to be no good reason against its acceptance by English and American zoologists. There is no single English word which expresses so tersely, clearly and characteristically the function of this structure. Precedant for the adoption of a foreign word in our terminology is not lacking. I refer to only one well known example. It is the word "Anlage" which is in current use universally.

Two variations of "Schluckapparat" are known in Cestoda, one a simple one composed only of annular muscles, and the other more complex and adding longitudinal muscles to the annulars. In *macrobothrium* only the simple type is found.

The vagina (Fig. 6) can be traced from the ovary forward along the median line where it lies as a small tube with short sinuous curves to the base of the cirrus sac. It there turns abruptly towards the margin and, in some preparations, can be traced right along the cirrus sac. The vagina appears to open immediately beside the cirrus, between it and the margin. It will, therefore, be correct to say that the vagina opens right under the cirrus but a little dorsal to it.

The shell gland (Fig. 8) consists of a very large number of club-shaped glandular cells whose fine deferent tubules lead in the region of the yolk sac into the oviduct. The cells of the shell gland are developed all around the oviduct. The cells themselves show the nucleus in a homogeneous protoplasm. There is evidence of an investing membrane around each cell.

The direct prolongation of the oviduct beyond the shell gland is the uterus. It is presumed that its original purpose

was the transportation of the finished eggs. But the multiplication of the number of eggs formed necessitated an elongation and widening of the transporting canal. This was undoubtedly the origin of the turnings and twistings that we now find. By far the most important question concerning this structure is that which has to do with the uterine openings for the extrusion of the ripe eggs. The uterus may be considered as a tube consisting of three or more hardly distinguishable parts. The first portion is that which begins with the shell gland and runs along as a rather thin tube. Then comes a much wider and convoluted portion carrying eggs. During the period of sexual maturity this portion is so overdeveloped as actually to crowd all the other organs. The final portion is that tube which connects with the exterior. Now the question arises, is there a real preformed uterine opening or not? If there is no such opening, then we have to explain how the mature eggs reach the exterior. In *macrobothrium* there is certainly no indication of a preformed opening. An inspection of the ruptured segments, and especially of the ruptured margins, will make this plain. What really happens in our species is this. The uterus ruptures, and that always at a definite spot, which is the same for all segments, and is always in the median line and on the ventral surface of the segment. The bursting of the uterus might be occasioned by contact, or by chemical or mechanical stimulus, however light. It is very commonly known that a mere dipping of the strobila into water will cause a bursting of the uterus and the evacuation of the eggs in a veritable stream. If the ruptured wall of the segment be carefully examined, it will be seen that there is no histological basis for the assumption of a performed uterine opening. The tissues are simply torn asunder. The same tissues, in the same position and order, appear on either side of the tear. The two severed sides can be brought together and there will be not the slightest trace to show where they had been separated. The rupture takes place in the ventral surface because that is the location of the uterus.

In conclusion the following list of specific characteristics is offered for *Stenobothrium macrobothrium*, in so far as a preliminary study will warrant the drawing up of such a list.

(1) An anapolytic strobila with all the segments even the last wider than long.

(2) A pars bothridialis representing the most excessive elongation known among Tetrarhynchoids.

(3) A thick muscular band running medially throughout the entire length of the individual on both dorsal and ventral surfaces.

(4) A double layer of muscles at either end of each segment.

(5) A many-branched excretory system whose branches meet again as continuations,—the inclosed spaces forming islands.

(6) A complicated canal system of the excretory apparatus which discharges into a metameric bladder in each segment.

(7) A marginal genital cloaca, situated anteriorly and ventrally.

(8) The vagina opening beside the cirrus, under it and dorsal.

(9) No preformed uterine openings.

(10) Nucleoli in the larger germ cells.

EXPLANATION OF PLATES.

The entire ten figures refer to the same species,—*Stenobothrium macrobothrium*, Diesing. The host is *Carcharias lamia*.

The same letters refer to the same structures throughout.

A M——annular muscles
Bl——bladder
C S——cirrus sac
E——excretory system (main trunk)
e——excretory system (small trunk)
L M——longitudinal muscles
M M——median muscle
N——nerve
Ov——ovary
Schla——schluckapparat
Sg——shell gland
Te——testes
Ut——uterus
Vag——vagina
Vd——vas deferens
Yg——yolk gland

FIG. 1. Entire specimen preserved in alcohol. It is a young specimen and shows the primary end segment. Scale: value of one space 50 mm.

FIG. 2. Proglottids showing extruded cirri and uterine openings, median and in a straight line. Scale: value of one space 100 mm.

FIG. 3. Head. Illustration shows proboscides, bothridia and collar. Scale: value of one space .05 mm.

FIG. 4. Cross section through a proglottis showing nerve, large and small excretory branches, yolk gland and testes. The section shows especially the strong ring of annular muscle and the cut ends of longitudinal muscles. Scale: value of one space 0.01 mm.

FIG. 5. Cross section through the region of the excretory bladder. The section shows the musculature of the periphery as well as the muscles of the septum. MM shows the large typical median muscle with Bl, the bladder.

FIG. 6. A cross section through the region of the cirrus sac to show the relative positions of cirrus and vagina. In this region the uterus is entirely absent.

FIG. 7. A cross section showing the schluckapparat, Schla., with an ovum included. The section shows the relative positions of this organ, uterus and ovary.

FIG. 8. A cross section showing the position of the shell gland, sg.

FIG. 9. A cross section of a proglottis showing the typical H structure of the ovary. The descending ramus of the right side is so thin that only a single egg can pass at one time.

FIG. 10. A cross section showing the ruptured uterus.

(Scale for Figs. 4 to 10: value of one space 0.01 mm.)

Fig. 1.

Fig. 2

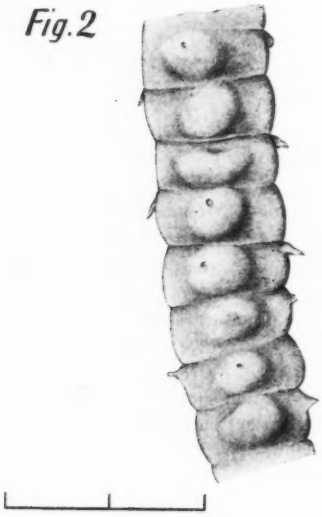


Fig 3

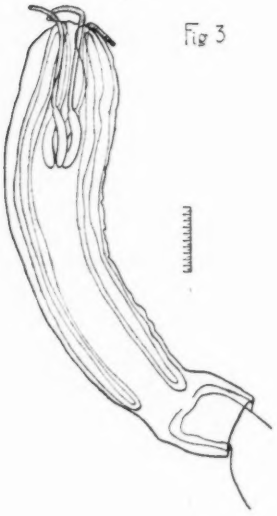
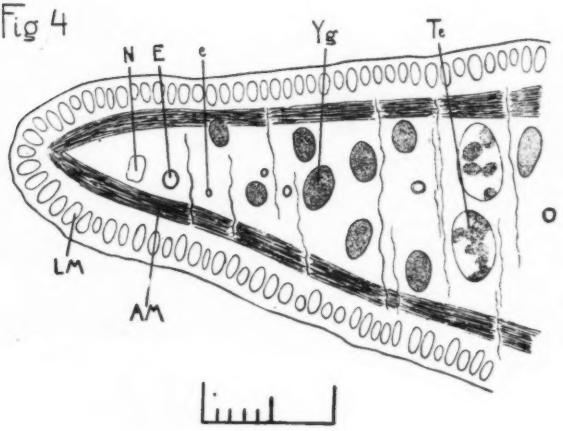


Fig 4



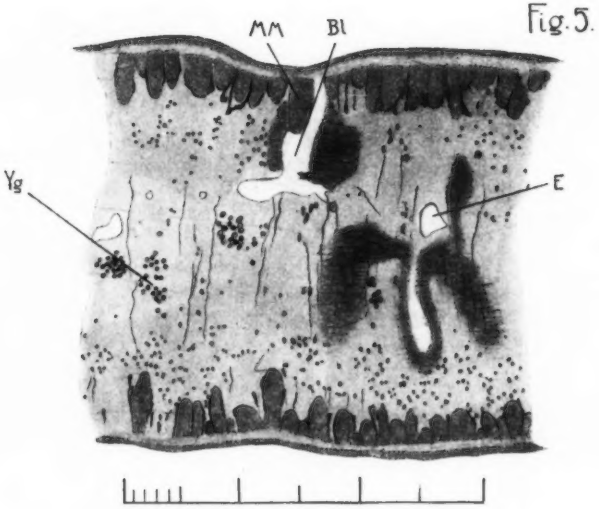


Fig. 5.

Fig. 6.

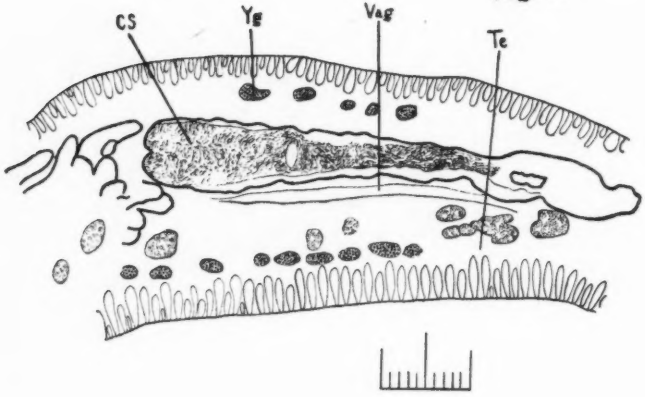


Fig. 7

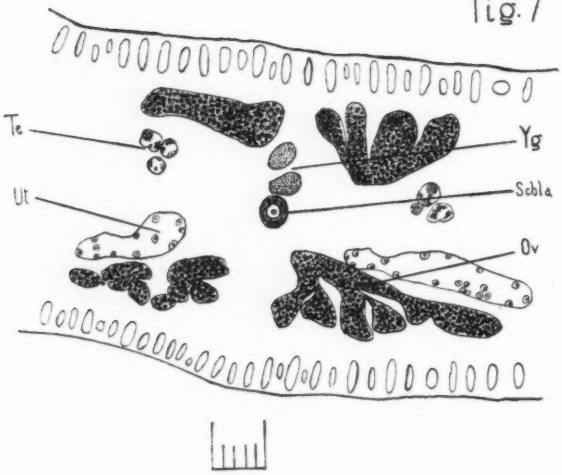


Fig 8.

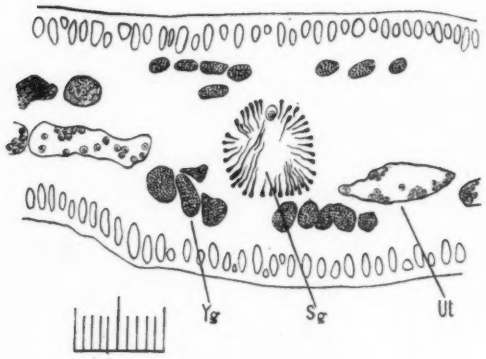
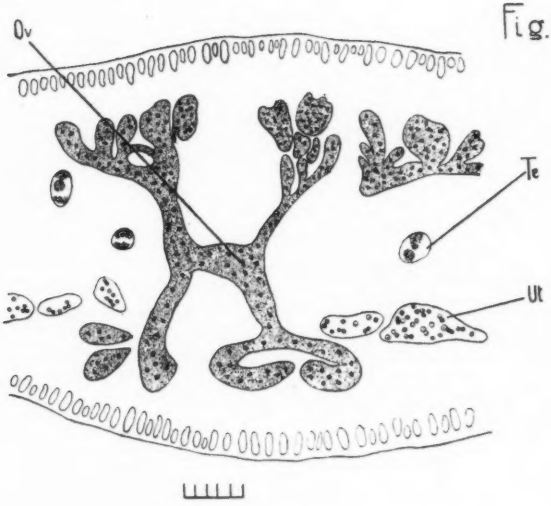
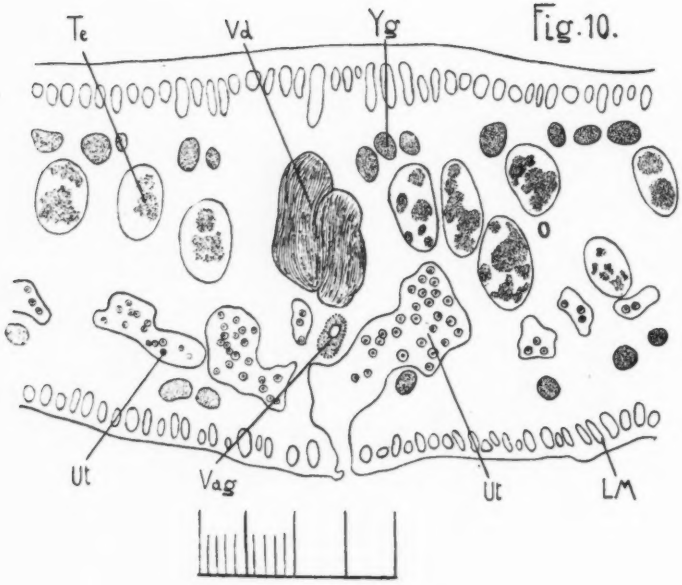


Fig. 9.




Te
Vd
Yg
Fig.10.
Ut
Vag
Ut
LM

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EQUISETITES IN POSITION OF GROWTH IN THE SUNDANCE LIMESTONE.[1]

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Cambridge, England.

I. INTRODUCTION.

Whilst examining the lower beds of the Sundance Formation near Thermopolis, Wyoming, my attention was attracted by a thin bed of limestone, perforated at right angles to the bedding by numerous tubular holes. These holes are generally 0.5 cm. or a little less in diameter, and are spaced at about 16 per square decimeter. At first glance they might be mistaken for worm burrows, but several peculiarities led me to suspect that they were not of that nature. In the first place, although most of the holes are about 0.5 cm. in diameter, they include quite an appreciable number of much smaller ones; on closer examination it was seen that narrow, thread-like holes branch out horizontally from the larger vertical ones. Secondly, the spacing of the larger holes is fairly regular—more so than would be expected in the case of worm

[1] These observations were made during the 1928 American Trip of the Princeton Summer School of Geology and Natural Resources, this paper being Contribution No. 6 of the School.

burrows. Thirdly, the bed has a very strong resemblance in appearance to certain plant bearing rocks which are familiar in delta deposits, for example, the "pencil gannister" of Yorkshire, England. This last resemblance was so striking that it led me to examine the limestone for recognizable traces of plants, and after a brief search, I found a thin layer in which the recumbent stems of a species of *Equisetites* were preserved in abundance.

The limestone with *Equisetites* lies at the base of the Sundance, and forms the crest of the ridge between the outcrops of the Chugwater Red Beds and the overlying shales of the Sundance Formation. The details of the section are as follows:

Section at the Base of the Sundance Formation near Big Horn Hot Springs, Thermopolis, Wyoming.

3.	Fine grained, thin bedded limestone, with broken shells of Gasteropods at the base	4′	6″
	c. Limestone with vertical holes	1′	2″
2. Equisetites Bed.	b. Layer with vertical stems of *Equisetites*	—	—
	a. Limestone with vertical holes	0′	5″
1.	White limestone, fissile at the top, about	3′	0″
	Chugwater Red Beds (contact unexposed)		

The full section at Big Horn Hot Springs has been measured and described by W. T. Lee.[2] The contact between the lowest member of the Sundance Formation (Jurassic), and the top of the Chugwater Red Beds (Triassic), was not seen at the spot where the specimens of *Equisetites* were collected; the basal bed (No. 1 in the section above) can hardly be more than a few feet thick, however. The actual contact

[2] W. T. Lee: Correlation of Geologic Formations between East-Central Colorado, Central Wyoming, and Southern Montana; U. S. G. S. Professional Paper No. 149, p. 57, 1927.

is discussed by Lee in the light of evidence from other exposures, and is thought to be unconformable.[3]

The bed which contains the vertical markings produced by *Equisetites* is a rather rough textured but well bedded limestone. The layer with recumbent aerial stems is about five inches from the base of the bed, and in places may be seen to be resting upon a surface of mud-cracks, filled in with a white pasty limestone. The presence of the Gasteropod *Neritina* (if it is correctly identified)[4] in the limestone immediately above the plant remains is strong evidence of brackish water or alongshore conditions. Although no shell fragments have been found in the beds numbered 1 and 2, the preservation of desiccation cracks and the undisturbed character of the sequence suggests that the conditions of formation of the sediment of these beds cannot have been much different from those which held during the formation of bed 3, and the environment was essentially the same. Thus, although the plants may have grown in an ooze not completely saturated with brackish water, or even on an emerged flat, their environment was maritime and not inland.

II. DESCRIPTION OF PLANT REMAINS.

The material available is not sufficiently complete for specific determination, but the fragments at hand are characteristic enough to leave no doubt that they belong to a species of *Equisetites*. This name is used in the absence of cones, internal structure, or other diagnostic features, since the stem impressions alone do not warrant inclusion in the genus *Equisetum*, which implies a very definite structure of the reproductive shoots and of the tissues of the stem. The generic name *Equisetites* was proposed by Sternberg[5] as a designation for fossil stems bearing a close resemblance to

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[3] W. T. Lee: ibid., pp. 15 and 16.

[4] W. T. Lee: ibid., p. 57.

[5] Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt, Fasc. VIII, p. 43. Leipzig, 1838.

recent species of *Equisetum*,[6] to which category the material under discussion naturally belongs.

The *Aerial Shoots* are represented by impressions of flattened stems. In the most complete specimen (No. 205, Fig. 4), which shows three nodes, the width of the stem is 1.3 cm. and the distance between successive nodes is 1.9 cm.

The *Leaf Sheath* consists of twenty or more sharply pointed segments, 0.9 cm. long in specimen 205 and 1.4 cm. in number 206; they are free for about half of their length. In many of the specimens the impression of a single vein can be made out. The actual position of the node is not always distinctly visible in the specimens available, and the conspicuous markings on the impressions are tips of the leaf sheaths.

The *Vertical Underground Shoots* are generally 0.3-0.5 cm. in diameter, and are preserved as cylindrical pipes, sometimes filled in with a white or pale buff powdery limestone, but are frequently found as empty cavities in the rock. The tubes occasionally show constrictions, which may indicate the positions of nodes. Roots are given off at right angles to the vertical shoots, and are generally preserved as narrow, thread-like holes in the limestone. (See Fig. 1.) Horizontal rhizomes and tubers were not observed.

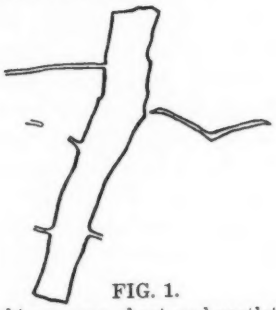

FIG. 1.

Equisetites, sp. Subterranean shoot and rootlets exposed on the fractured surface of the rock. Specimen No. 202, x1.5.

[6] See also Seward, Fossil Plants, Vol. I, p. 257, 1898.

From the manner in which these fossils occur in the rock, there can be little doubt that they were actually growing on the spot where they are now found. There is no trace of soil, and the roots run out into a matrix which, on analysis, is found to be 90-93 per cent fine grained calcium carbonate, and must have been a soft carbonate ooze when the plants were growing—otherwise it could not have preserved their impressions.

III. COMPARISON WITH THE VEGETATION ON MODERN DREWITE FLATS OF THE BAHAMAS.

The main point of interest which this occurrence of *Equisetites* presents is the close resemblance between the conditions under which the plants must have grown at Thermopolis in Jurassic times, and the peculiar conditions under which various plants, especially the Mangrove, *Rhizophora mangle* L., grow at the present day on certain islands on the Great Bahama Bank.

The Bahama Bank forms a large area of shallow water (for the most part ten to fifteen feet deep) completely surrounded by deep water.[7] The marine deposits of the Bank are entirely calcareous, and consist largely of Drewite, a very pure and fine grained calcium carbonate mud. Large areas of the islands on the Great Bahama Bank are formed of raised deposits of the same material. The western part of Andros, and the two small islands, Billy and Williams, which lie to the west of Andros, are devoid of soil, and are covered with a glaring white, heavily sun cracked surface of Drewite. Through this deposit the Mangroves grow (see Fig. 6), and where they are colonizing new ground, the underground rhizomes send up a thick growth of new shoots, about the size of pencils. (See also the figure on p. 53 of Agassiz's paper.)

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[7] For descriptions of the Great Bahama Bank, see Alex. Agassiz, Bull. Mus. Comp. Zool. at Harvard Coll., Vol. XXVI, No. 1, pp. 17-62, esp. pp. 50-56, 1894; R. M. Field, Am. Journ. Sci., Vol. XVI, No. 93, pp. 239-246, 1928.

This is the state of affairs over the botanical region known as the "swash" or "marl"[8] which includes most of the Western half of Andros Island, and the smaller islands immediately to the west. The resemblance between these stretches of soil-less Drewite with their vertical mangrove shoots, and the Sundance limestone at Thermopolis, with its vertical shoots of *Equisetites*, is very close.

It has been suggested that, since modern species of *Equisetum* secrete considerable quantities of silica, and related Jurassic plants may have done the same, the latter would have been in difficulties through growing in a medium consisting largely of calcium carbonate. It may be pointed out that the silica must enter the plant in solution, whatever the environment may be; and since there is sufficient silica in solution in sea water to provide material for the skeletons of siliceous organisms[9] there would no doubt be enough to satisfy the demands of *Equisetaceous* plants. It is also perhaps worth mentioning that Drewite is over 99 per cent, whilst the limestones at Thermopolis range between 90 and 93 per cent calcium carbonate.

IV. COMPARISON WITH THE OCCURRENCES OF EQUISETITES IN SILTY BEDS OF JURASSIC AGE.

A comparison which at first sight seems remote, but is perhaps actually of some significance, is with the similar manner in which other species of the same genus occur in shaley and silty beds. In the delta deposits of the Middle Jurassic of Yorkshire, England, are numerous beds of silt which con-

[8] The botanical regions of Andros Island are discussed by Mrs. Northrop in The Flora of New Providence and Andros, Mem. Torrey Botanical Club, Vo. XII, No. 1, pp. 4-8, 1902; and by Small and Carter, Report on Botanical Exploration in Andros, Bahamas, Journ. N. Y. Bot. Garden, ol. XI, No. 124, pp. 88-101, 1910.

[9] There also is evidence on some parts of the Bank to show that silicification of calcareous material has taken place on land, showing the presence of silica locally in the ground water.

tain stems and roots of *Equisetites columnaris* Brongn. and *E. beani* (Bunb.) in the position of growth.[10] The remains of the plants are found as vertical pencil-like rods in the laminated silts through which they grew, and also as flattened recumbent stems. These silts have a very characteristic appearance, which is closely parallelled by that of the *Equisetites* Bed in the Sundance formation, and the conditions may, to some extent at least, have been comparable. There is little previous evidence to show that plants of this genus grew either in a salt water or a marine tide flat environment, or in carbonate oozes. All the associations of these fossils have been presumed to be with fresh water or terrestrial plants, though in some cases the communities may be better interpreted as those of a salt marsh. For example, Dr. Hamshaw Thomas[11] has shown on physiological and ecological grounds that some of the plant beds of the Yorkshire Estuarine Series are probably the remains of salt marsh communities, and it is possible that some of the beds of the same age which contain nothing but *Equisetites* may have originated similarly. Dr. Halle has definitely made this suggestion in describing an occurrence of upright stems and horizontal rhizomes at Ravenscar, Yorkshire. He is of the opinion[10] that "*Equisetites* grew in large, shallow, fresh or brack-water lagoons or protected estuaries with low marshy shores . . ." If this be so, the parallel is even closer, although the remarkable fact remains that in one case the plants grew in a fine argillaceous mud devoid of lime, and in the other they grew in a fine grained mud consisting largely of calcium carbonate.

I am much indebted to Mr. J. Bridge and Mr. J. T. Sanford of the Department of Geology, Princeton University, for preparing the photographs for this paper, and to Mr. W. N.

[10] For description and figures of a typical example, see Halle, Geol. Mag., pp. 3-7, 1913; and Kendall, Geol. Mag., pp. 7-9, 1913.

[11] In his Sedgwick Prize Essay on the Yorkshire Estuarine Series (unpublished).

Edwards of the British Museum (Natural History), for reading the manuscript and making several suggestions.

EXPLANATION OF FIGURES

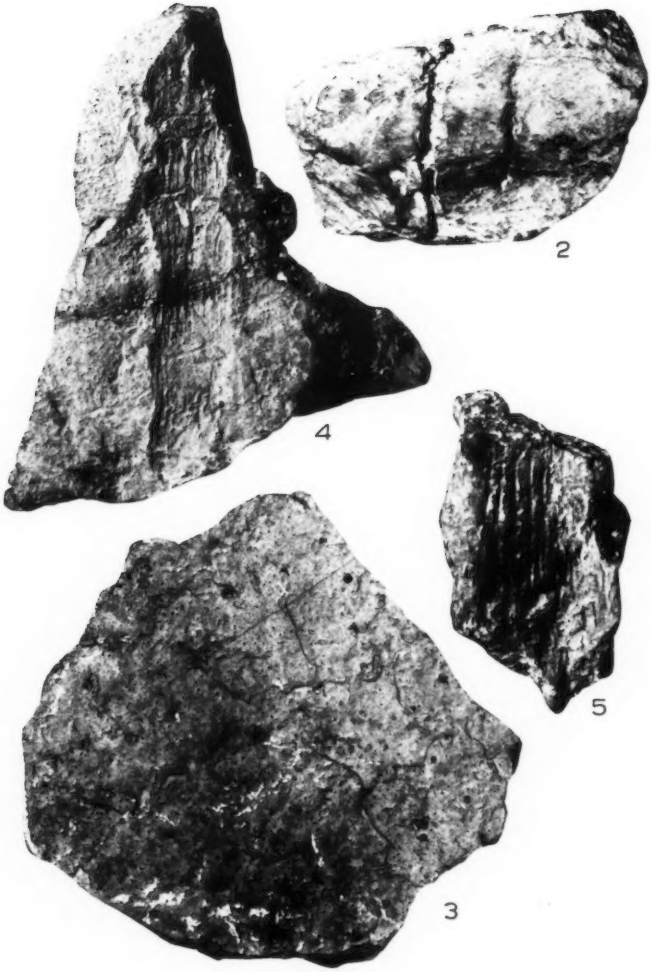
Figs. 2 and 3.—Limestone with vertical holes (subterranean shoots of *Equisetites.*) 2. Vertical section, showing form of shoots. Specimen No. 203 x5/6. 3. Cross section, parallel with the bedding, showing spacing of the holes. Specimen No. 204 x 0.5.

Fig. 4.—*Equisetites* sp. Stem impression showing three nodes and internodes. Specimen No. 205 natural size.

Fig. 5.—*Equisetites* sp. Single node and leaf sheath. Specimen No. 206 x 5/3.

Fig. 6.—View of the "swash" or "marl" region, Williams Island, Bahamas. The bushes are half-grown Mangroves, and the pencil shaped shoots grow from rhizomes of these plants. This is typical of the islands on the central part of the Great Bahama Bank.

Fig. 7.—Detailed view of the surface of the ground in the "swash" of Williams Island, showing the complete absence of soil on the sun cracked surface of Drewite.



FIGURES 2-5

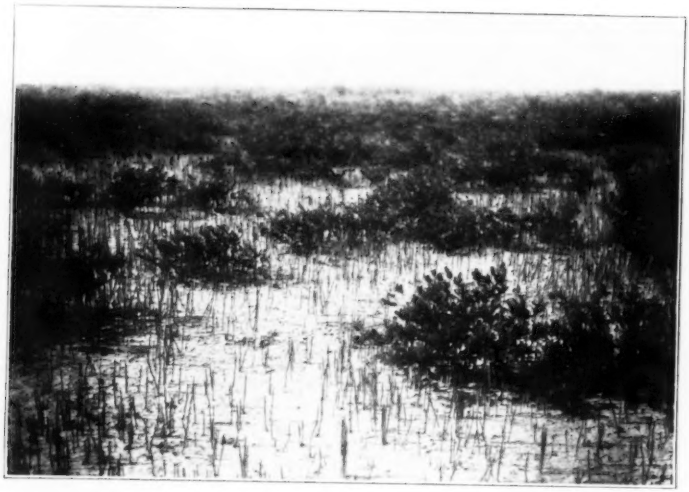


FIGURE 6

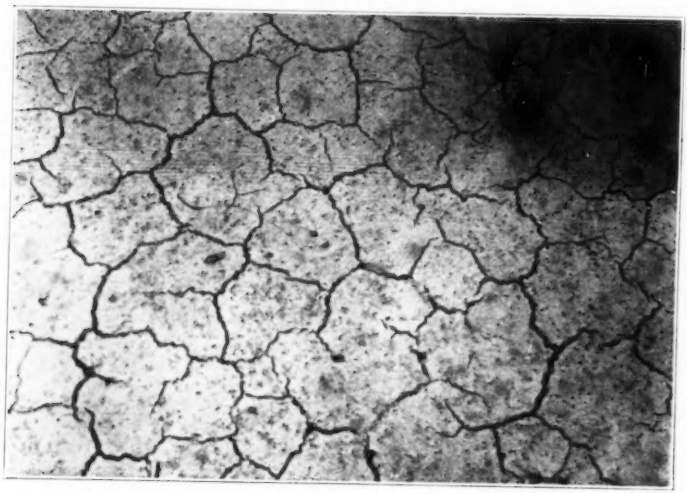


FIGURE 7

NOTE

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